

Cooperation vs. exploitation: interactions between Lycaenid (Lepidoptera: Lycaenidae) larvae and ants

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Abstract. The larval stages of many lycaenid species are myrmecophilic, i.e. they are associated with ants. We revised the literature and categorized these associations as neutral (nonexistent, commensalistic), cooperative (mutualistic, mutualistic inquiline), and parasitic (food competitor, cleptoparasitic, predaceous symphile, or synechthran). The relationships were also noted as being facultative or obligate. Within several of the lycaenid taxa there has been a change in the diet from phytophagy to aphytophagy associated with a change from cooperative to exploitative behavior towards ants. A relatively low number of species, however, seem to have followed the route from cooperative (mutualists) to exploitative behavior (cleptoparasites, predaceous symphiles, synechthrans) even though the latter may give higher returns for less investment. Even neutral behavior (no relation with ants, commensals) is more probable than exploitative behavior. We suggest that this pattern reflects both the constraints produced by the species specific nature of exploitative interactions and the stability of cooperative interactions in evolutionary terms. We suggest that a “reverse evolution” from obligatory to facultative relationships is evolutionarily unlikely, a phenomenon which may be explained by negentropy criteria or the irreversible nature of evolution.

INTRODUCTION

Many species of lycaenids are myrmecophilic, i.e., they are associated with ants. Through these associations with ants, lycaenid larvae have developed a number of morphological and behavioral adaptations. Many species of larvae have evolved what have been termed myrmecophilous organs, one of the most important of these being the nectary organs which are found on the seventh abdominal segment and secrete a substance containing sugars and amino acids when solicited by the ants (Malicky 1970, Maschwitz et al. 1975, Pierce 1983, Cushman et al. 1994).

Apart from their morphological adaptations lycaenid larvae are unusual with respect to their diet. They may feed on lichens, homoptera, or ant brood rather than on angiosperms, which is the normal food of lepidopterous larvae. Many of the interactions involving lycaenid larvae and ants have been described (Kitching 1987; Fiedler & Maschwitz 1988, 1989a, Elmes et al. 1991) and a exhaustive revision of these was undertaken by Fiedler (1991b). Lycaenid-ant interactions have been classified as mutualistic/para-

sitic, facultative/obligate and phytophagous/aphytophagous. Although some authors (Henning 1983) have given finer classifications, the full range of possible associations have not been taken into account. For example, *Maculinea* spp. and *Liphrya brassolis* are both classed as "parasites" even though they have completely different relations with their ant hosts at a behavioral level which implies different evolutionary pathways towards each of these two types of relation; *Maculinea* spp. are attended, for example *M. alcon*, *M. rebeli* (Cottrell 1984, Elmes et al. 1991), or ignored, for example *M. arion*, *M. teleius* (Cottrell 1984), by the ants whilst *Liphrya brassolis* is attacked (Johnson & Valentine 1986).

Several authors have studied the relative importance of cooperation vs. exploitation using different models and have shown that in theory, "cooperation rather than "exploitation" dominate in the Darwinian struggle for survival" (Nowark & May 1992, Nowark et al. 1996, Sigmund 1992). Empirical evidence suggests that in the Lycaenidae this dominance of cooperation over exploitation may be true (Pierce 1987, Fiedler 1996).

Using data in the literature, most of it summarized by Fiedler (1991a, b), on the types of interactions between lycaenid larvae and ants, the myrmecophilous organs on the lycaenid larvae, the degree of relationship (facultative or obligate) and the diet of the larvae, we tentatively propose a more detailed classification of "types of interaction." In each case we noted the presence or absence of the nectary organs, larval diet (spermatophytes, algae, lichens; homoptera; ants; homoptera honeydew; ant regurgitations), and type of interactions with ants. Using this information we classified eight types of interactions the larvae may have with the ants. We then use this classification to describe the diet changes that have occurred both between and within subfamilies (from phytophagy to aphytophagy) and discuss these diet changes in the context of the relative importance of cooperative/exploitative behavior of the larvae towards their ant partners.

A truly phylogenetic system of the Lycaenidae is still not available, thus the diet changes we describe cannot yet be confirmed since without a sound phylogeny the directionality of such changes is difficult to assess. Nevertheless, it is widely considered that phytophagy is a primitive trait in lycaenids (and butterfly larvae as a whole) (Cottrell 1984, Fiedler 1991b), thus we feel justified in our assessments of possible evolutionary change from phytophagy to aphytophagy in the Lycaenidae. The higher classification of the Lycaenidae we adopt is the same as that used by Fiedler (1991b), based on Eliot (1973), with modifications by Scott and Wright (1990). The discussion about whether or not the Riodinidae (or Riodininae) form a monophyletic group together with the Lycaenidae is still very much alive (Robbins 1988, De Jong et al. 1996, Weller et al. 1996), but since the myrmecophilous organs of the Riodinidae are clearly analogous but not homologous with those of the Lycaenidae (DeVries 1990) we do not further discuss the Riodinidae here.

TYPES OF INTERACTION BETWEEN LYCAENID LARVAE AND ANTS

The range of types of relationships that the ants may share with lycaenids

were classified as follows. It must be emphasized that these are “types of behavioral interactions,” not “types of larvae.” Thus a larva that is neutral at one stage of its life cycle may be parasitic at another, as in *Maculinea* spp. (Cottrell 1984). Parasitic larvae such as *Maculinea rebeldi* or *M.alcon* may be generally regurgitation feeders (cleptoparasites) but during times of food shortage may also prey on eggs and ant brood (Elmes et al. 1991).

Relationship not recorded

Larvae which have unknown relationships with ants. (Relationships recorded with a question mark by Fiedler [1991a, b].)

Neutral relationships

The ants neither gain nor lose from the interaction with the lycaenid larvae. The larvae, however, may neither gain or lose (No relationship) or may gain (Commensal) from the relationship. It is very difficult to assess with the data available which larvae are in “No relationship” with the ants, and which are “Commensals.” The discussion about whether the larvae enter into “enemy free space” or not must depend on studies of particular lycaenid larvae and their relation with ants. Whether or not the ants protect the larvae in any way from other predators depends on factors such as time of occupancy of ants at the site, whether or not they have antagonistic relations with the larvae, and whether they influence in the rates of predation or parasitism of the larvae. Since the subject of whether and which of these larvae benefit from the presence of ants is in many cases ambiguous we have lumped “No relationship” and “Commensal” into the same category of Neutral relationship. Nevertheless, it is useful to define the two sub-categories, as they may represent the transition from a completely myrmecoxenous state to the beginnings of an association with ants.

No relationship. The larvae do not interact with ants mutualistically, parasitically, or commensally. Thus neither the ants nor the larvae gain from the relation. The larvae may avoid encounters with ants using specific defensive tactics such as *Eumaeus atala* (Bowers & Larin 1989) or they may be rarely found by ants. The point is that they do not enter into ant-inhabited “enemy free space” (Atsatt 1981). In the Curetinae, ants sometimes encounter larvae and then lick up plant sap at feeding damage, or feed at extra floral nectaries (DeVries et al. 1986, Fiedler et al. 1995). The evidence is ambiguous, however, as to whether or not the larvae benefit from the relation.

Commensalistic. In these associations, unlike the “No relationship” associations, the larvae benefit from the relation, whilst the ants remain unaffected. Thus they gain a twofold advantage (avoidance of ant attacks and entering into “enemy free space”). Commensalistic relations have been described in the Liptenini where the larvae are strictly associated with ant columns on tree trunks where they feed on lichens or algae. The data are, however, scanty and the proportion of Liptenini in these types of relationships is unknown (Downey 1962, Atsatt 1981, Callaghan 1992). The larvae

Table 1. Number of species and relative proportions of neutral, cooperative, and exploitative interactions found between lycaenid larvae and ants: a) within the subfamilies of the Lycaenidae, b) within the Lycaeninae.

a)	Poritinae		Miletinae		Curetinae		Lycaeninae			
	Liptenini	Miletini	Liphryini	Curetini	Total	%*	Grand Total	%*		
Not recorded	0	0	0	0	0		122	122	—	
Phytophagous										
Neutral	60	0	0	7	67	64.4	215	283	30.8	
Cooperative	0	0	0	0	0		574	574	62.5	
Aphytophagous										
Exploitative	0	28	9	0	37	35.6	24	61	6.7	
Total	60	28	9	7	104	100	935	1039	100	
b)										
	Lycaeninae									
	Aphnaeini	Lycaenini	Theclini	Eumaeini	Polyommattini	Total	%*			
Not recorded	4	0	0	104	14	122	—			
Phytophagous										
Neutral	5	38	44	101	27	215	26.5			
Cooperative										
Facultative	18	0	57	111	284	470				
Obligate	49	0	19	2	34	104				
Total Cooperative	67	0	76	113	318	574	70.5			
Aphytophagous										
Exploitative	4	0	4	0	16	24	3			
TOTAL	80	38	124	318	376	936	100			

*The last column (%) refers to the relative proportion of lycaenid larvae in a given type of interaction with ants with respect to the total number of larvae. Larvae with a relation "not recorded" are NOT taken into account.

supposedly gain from the relation in that the presence of ants reduces attacks from predators and parasites (Atsatt 1981) whilst the ants remain unaffected since the larvae do not compete in any way with food or other resources. Nonetheless, Callaghan (1992) described larval behavior in 12 species from the tribe Liptenini where the larvae seem to have strictly defensive relationships with ants, thus suggesting that the ants may not be protective elements in this case and that the relationship between them and the larvae is rather antagonistic. Nevertheless, detailed studies are required in order to establish exactly what is the relationship between the ants and certain Liptenini larvae. There are also certain species in the Lycaeninae that can be classed as being commensalistic because they are or appear to be associated with ants, but apparently do not possess a nectary organ and thus presumably do not provide the ants with a substantial food resource, for example *Aloeides dentatis* (Henning 1983).

Mutualistic (Cooperative)

This follows the standard definition of mutualism in the literature whereby both the ants and the lycaenid larvae benefit from the association. The larvae secrete a sugary nectar which the ants imbibe (Fiedler & Maschwitz 1988, 1989a, Cushman et al. 1994, Fiedler & Saam 1995). The ants in return protect the larvae from predators and parasites (Pierce & Mead 1981, Pierce et

al. 1987, Baylis & Pierce 1991) Under this definition a larva is mutualistic if it has a functional nectary organ, if the diet is phytophagous and if it is associated with ants. Mutualists may be facultative or obligate, where the term obligate is defined as complete dependency on a specific genus of ants (Fiedler 1991b, 1994). Mutualists as defined here are only found in the Lycaeninae (Table 1).

Mutualistic inquiline. Here we define a new type of interaction which is a subdivision of the mutualists. In this case the larvae are attended by ants as for the mutualists, but furthermore they shelter either in pavilions constructed by the ants or in the ant nests themselves. The larvae, however, remain phytophagous, leaving the shelters to feed on their hostplant. Examples of species which exhibit “inquiline behavior” are *Anthene emolus* (Fiedler & Maschwitz 1989a) and *Paralucia aurifera* (Cushman et al. 1994). It must be emphasized again that it is the interaction that is important not the species. Thus “inquiline behavior” may be a rare occurrence in a species or a life history trait. The importance of this category is that it suggests a possible intermediate stage between free-living mutualists and parasites which live in the ant colony and feed on the ant brood.

Parasitic (Exploitative)

In these cases the lycaenid larvae benefit from the association whilst the ants are disadvantaged. We divide the parasitic larvae in four subgroups; food competitors, cleptoparasites (after Hoelldobler & Wilson 1990), predaceous symphiles and synechthrans (after Wasmann 1894).

Food competitors. Here we define a type of interaction in which the larvae feed on Homoptera (and Homoptera secretions), which have a trophobiotic relationship with ants such as many species from the Miletinae (Kitching 1987, Maschwitz et al. 1985, 1988). This definition differs from that of Maschwitz and Fiedler (1988) who defined homopterophagous lycaenid larvae as “indirect parasites.” We suggest, however, that “food competitors” is a more precise definition. The food competitors may be further divided into “stealthy competitors,” which are not tolerated by the ants and feed inside shelters or cover themselves with bits of their prey to protect themselves from ant attack, for example, *Spalgis* spp., and “symphylic cleptoparasites,” which are ignored or even sometimes attended by the ants, for example, *Miletus* spp. (Cottrell 1984, Fiedler 1991b).

Cleptoparasites. The larvae are food robbers (*Euliphyra* spp. [Dejean & Beugnon 1996]) or feed on oral regurgitations from ants. Oral regurgitation feeders may be either free-living (*Spindasis takanonis*) or may inhabit the nests of the ants (*Niphanda fusca*) (Cottrell 1984). Fiedler (1991b) defined ant regurgitation feeders as “parasites,” nevertheless Hoelldobler and Wilson (1990) define “food robbers” which rob the ants of a food resource and the regurgitation feeders which receive nutrients that would normally be destined for the ant brood (oral regurgitations) as cleptoparasitism (cleptobiosis in their terms). Cleptoparasitic behavior has been reported from both the Lycaeninae and Miletinae.

Predaceous symphile. The larvae spend all or part of the larval phase inside the nests of their host ant, feeding on ant brood. By means of putative pheromone secretions the larvae are accepted by the ants as ant brood whilst they remain in the ant nest (Jackson 1937, Cottrell 1984, Thomas et al. 1989). This definition applies to lycaenids such as *Maculinea arion*, *M. teleius*, and *Lepidochrysops* spp., described simply as "parasites" in the literature, for example (Cottrell 1984, Elmes et al. 1991).

Synechthran (following Wasmann 1894). These species of lycaenid also feed on ant larvae, but their relation with the ants has a completely different behavioral base than that of the predaceous symphiles. The larvae are not welcome guests in the ant nests; rather they are treated as intruders and attacked by the adult ants. *Liphyra brassolis* (Johnson & Valentine 1986) is apparently the only known case which falls in this category in the Lycaenidae.

CHANGES IN THE DIET WITHIN SUBFAMILIES

Changes in the diet within a subfamily have taken place in the Lycaeninae from angiosperms to ant brood, Homoptera and regurgitations from ants, and in the Miletinae from Homoptera, to honeydew, ant regurgitations, or ant brood.

Changes in the diet in the Lycaeninae

Within the Aphaenini, Theclini, and Polyommataini there has been a change in the diet from phytophagy to aphytophagy, the aphytophagous larvae feeding on Homoptera (food competitors) or oral regurgitations from the ants (cleptoparasites), but sometimes on ant larvae or pupae (predaceous symphiles). The phytophagous species in the Lycaeninae are either commensals (e.g., *Aloeides dentatis*; all examples taken from Fiedler [1991b] unless otherwise stated), mutualists, mutualistic inquilines, or have no relation with ants. Their behavior towards the ants is thus neutral or cooperative. The aphytophagous species, however, all exploit their ant hosts. Food competitors and/or cleptoparasites may be found in the Aphaenini, (*Spindasis nyassae*, *S. takanonis*, *Axiocerses harpax* and *A. pseudo-zeritis*, oral regurgitations), in the Theclini (*Shirozua jonasi*, oral regurgitations) and the Polyommataini (*Niphanda fusca*, oral regurgitations, *Triclema lamias*, Homoptera and three *Maculinea* spp.). These species have nectary organs and sometimes also tentacle organs (except *S. jonasi*, which has neither). There are predaceous symphiles in the tribes Theclini: *Acrodipsas cuprea*, *A. myrmecophila*, *A. illidgei*; Polyommataini: two *Maculinea* spp. and nine *Lepidochrysops* spp.; and Aphaenini: *Cigaritis acamas* (Sanetra & Fiedler 1996). As far as is known, all species possess a nectary organ, except *Cigaritis acamas* which also has eversible tentacles. The *Maculinea* spp. are generally specific to one ant species, at least within the same geographical region (Thomas et al. 1989). *Lepidochrysops* spp. are almost certainly species specific (Cottrell 1984), although there is little information as regards the remain-

ing genera, what evidence there is points to host-ant specificity (Cottrell 1984).

Changes in the diet within subfamilies in the Miletinae

In the Miletinae there have been changes in the diet of the larvae from Homoptera to other food sources (all examples taken from Fiedler [1991b] unless otherwise stated). Although the scarcity of data on this tribe does not permit conclusions to be drawn we can state that in all cases studied the behavior of the larvae towards the ants is exploitative. In the Miletini there are several species reported to feed on Homoptera honeydew, these include *Miletus chinensis*, *Taraka hamada*, *Logania malayica*, *L. marmorata* (also Homoptera) (Fiedler 1993), *Allotinus unicolor* (also Homoptera) (Maschwitz et al. 1985, Fiedler & Maschwitz 1989b) and *Lachnocnema bibulus* (also ant regurgitations). *Thestor* spp. (Miletini) are suspected of preying on ant brood. In the Liphyrini *Euliphya mirifica* and *E. leucyana* feed on oral regurgitations from ants and *Liphya brassolis* (Liphyrini) feeds on ant brood. These species do not possess nectary or tentacle organs. Of these, *Lachnocnema* is not specific as regards the ant host, but *Thestor*, *Miletus*, *Euliphya*, and *Liphya* are species specific.

DISCUSSION

Facultative and obligate relations in the Lycaeninae

Regarding the subfamily Lycaeninae, Fiedler (1991b) discusses the possible evolutionary development from facultative mutualisms to obligate relations of various types (including mutualists, inquilines, cleptoparasites, predaceous symphiles) or alternatively an evolutionary decrease in the interactions with ants (secondary myrmecoxeny). He states that there “is yet no evidence that a reverse evolution from obligatory towards facultative myrmecophily has ever occurred within the Lycaenidae, although such would be possible from theory.” We propose that the theory of negentropy provides a possible explanation for the lack of evidence for this “reverse evolution.” This proposal assumes that the higher the order or complexity of an organism, including in the concept of complexity higher specializations that may involve loss or simplifications of certain structures, the lower will be the probability state of the system and the longer the evolutionary time to produce the given state. Thus the further down a certain evolutionary pathway an organism finds itself the fewer available choices it will have to return back along that pathway (Zotin & Konoplev 1978, Jaffé 1984, Jaffé & Hebling-Beraldo 1993, Jaffé & Fonck 1994). We argue that obligate myrmecophiles are more “complex” in that they have more finely tuned adaptations in their associations with ants than facultative myrmecophiles. Thus in this case negentropy is expressed as specificity of communication with ants. (For a discussion on lycaenid/ant communication see Fiedler et al. [1996].) For example, the predaceous symphiles are often associated with one or a few ant species, which implies the development of brood pheromone mimics, that are specific to a single (or a few closely related) ant spe-

cies (Thomas et al. 1989), probably from facultative relations where the larvae are attractive to many species of ant. A reversal of this trend would imply a loss of specificity and thus of complexity, which would revert and thus probably reduce the adaptive gains made in the first place. This negentropic assumption does not exclude the possibility of posterior losses as has taken place in the secondarily myrmecoxenous species, but predicts that these reversions should be rare and should have specific biological explanations, as the evolutionary process is strongly irreversible (Jaffé 1996).

Cooperation vs. exploitation in lycaenid/ant relations

From Table 1, we may conclude that the majority of the lycaenid butterflies maintain neutral (no relationship, commensalistic) or cooperative (mutualistic) interactions with ants, rather than exploitative (cleptoparasite, predaceous symphile, synechthran) ones (Pierce 1987, Fiedler 1996). This fact seems remarkable considering that exploitative behavior may give higher nutrient returns for less investment to the lycaenid larvae. In subfamilies without a nectary organ, i.e. where cooperative behavior has not appeared (Table 1a), 64.4% of species show neutral behavior (no relation or commensal), representing the subfamilies Poritiinae (60 species) and Curetinae (7 species) and only 35.6% of the species show exploitative behavior (cleptoparasites or synechthrans) representing the Miletinae (37 species). In the Lycaeninae with 818 species (Table 1b, excluding species for which no information is recorded), cooperative behavior dominates, with 70.5% of the larvae being mutualists as opposed to 3% being cleptoparasites or predaceous symphiles. In this subfamily, 26.5% of the species have no relation with ants are or commensals, showing that even neutral behavior is more likely than exploitative behavior. Taking the Lycaenidae as a whole (Table 1a final column), 62.5% show cooperative behavior, 6.7% exploitative behavior and 30.8% neutral behavior towards the ants. Although these percentages may vary as more Lycaenid species are investigated, we suggest that the relative proportions between exploitative larvae and cooperative/neutral larvae should remain roughly the same.

Thus, where cooperative (mutualistic) behavior is possible in the Lycaenidae this is the most probable evolutionary outcome, and where it is not likely, neutral behavior is more probable than exploitative behavior. The preponderance for mutualistic interactions over exploitative relations in Lycaenidae lead us to suppose that cooperation must have either a higher probability to evolve or to be maintained during evolution or both. Thus, we postulate that cooperation is an evolutionarily more probable strategy compared to exploitative behaviors. We propose different, but not necessarily contradictory, explanations for this pattern:

- 1) A model of cooperation between species as a stable strategy was developed by Axelrod and Hamilton (1981) using the Prisoners Dilemma game. They showed that if the probability that two individuals will continue to interact is great enough then cooperation may be evolutionarily stable. Since then several authors have modeled cooperation vs. exploitation using dif-

ferent versions of the Prisoners Dilemma and have shown that in theory, “cooperation rather than exploitation can dominate in the Darwinian struggle for survival” (Nowark & May 1992, Nowark et al. 1996, Sigmund 1992). Empirical evidence suggests that the Lycaenidae larvae benefit from the association (Pierce et al. 1987, Robbins 1991, Fiedler & Hoelldobler 1992, Wagner 1993) and there is evidence showing that both partners benefit (Fiedler & Maschwitz 1988, 1989a, Cushman et al. 1994, Fiedler & Saam 1995). Cooperation in lycaenid/ant interactions is not necessarily a fixed strategy (Bronstein 1994, Noe & Hammerstein 1994, 1995) and a coalition may end or change when it becomes unproductive for one or both partners (Enquist & Leimar 1993). For example, ants abandoned *Polyommatus coridon* larvae when the secretions from the nectary gland were artificially eliminated (Fiedler & Maschwitz 1989c). Leimar and Axen (1993) showed that the amount of nectar secreted by larvae of *P. icarus* varied according to the level of ant attendance and the larva’s need for protection. A model of mutualism, commensalism and parasitism as evolutionarily stable strategies in lycaenid/ant relations was developed by Pierce and Young (1986). This model assumes that the ants enhance both the population growth rate and the equilibrium density of the larvae by increasing the realized fecundity of individual butterflies and by increasing juvenile survival, whereas the larvae enhance the equilibrium density of the ants by increasing ant food supply. Under these assumptions (albeit largely unverified) Pierce and Young (1986) were able to demonstrate that all three types of relation were evolutionarily stable strategies. Nonetheless, although all three strategies are evolutionarily stable, not all have the same odds of appearing during evolution and of avoiding extinctions in evolutionary history. Cooperative strategies possess economic advantages which decrease their probabilities of extinction and thus increase their odds of being fixed in the genetic repertoire of more species. That is, cooperation is a highly probable strategy in addition of being evolutionarily stable.

2) There are three possible strategies for exploitative behavior which the larvae could take; a “synechthran” approach where the larvae fend off ant attack whilst predating on ant brood, a “stealthy” approach, whereby the larvae avoid ant attack, and a “sympilic” approach whereby the larvae deceive the ants by mimicking ant brood. Thus, ants either ignore the larvae or attend them as they predate on Homoptera or ant brood. Examples of the first approach could be *Liphrya brassolis* which has an armor shaped carapace in order to withstand ant attack. This type of defense does not, however, seem to have developed in lycaenid taxa other than the Liphyrini. Examples of the second “stealthy” approach may be found in the genera *Taraka*, *Spalgis*, and *Feniseca* (Miletini) where the larvae occupy silken tents or burrows, or cover themselves with remains of their prey to avoid ant attack (Cottrell 1984, Kitching 1987). The third “sympilic” approach involves the development of a chemical mimicry system with the larvae mimicking their homopteran prey, adult ants or ant brood. The possibility that lycaenid larvae are chemical mimics has been studied for *Aloeides dentatis*, a non-

mutualistic inquiline and *Lepidochrysops ignota*, a predaceous symphile (Henning 1983). In both species, larval epidermal glands produced a secretion that appeared to mimic the brood pheromones of the host ants, although Henning (1983) did not identify the chemical compounds involved. It is also supposed that *Maculinea* spp. mimic the brood pheromones of their *Myrmica* ant hosts (Thomas et al. 1989), although chemical analyses have not been undertaken as yet. In the Miletini many lycaenid larvae such as *Miletus* spp., *Lachnocnema bibulus* are attended by ants even though they do not give any reward (Cottrell 1984). All of these strategies; the "synechthran" approach, the "stealthy" approach and the "symphilic" approach carry with them certain disadvantages. The carapace used by *Liphyras brassolis* may not be 100% effective against all ant species, with the larvae possibly incurring high mortality rates as a result. This restricts the larvae to only associating with *Oecophylla* spp. The stealthy larvae may still be attacked by ants in spite of their protective burrows. The symphilic larvae are constrained by having to penetrate the complex chemical communication systems of ants, which are highly species specific. In this sense it is notable that the larvae mimic the brood of the ants rather than the adult ants. In the genus *Myrmica* (usually hosts for larvae of *Maculinea* spp.) the brood odor is not specific to one species and *Myrmica* brood are transferable between the nests of different species (Brian 1975, Howard et al. 1990), although Thomas et al. (1989) point out that these ants are far more discriminatory under conditions of stress.

3) As far as the "symphilic" or "mimicry" approach to exploitative behavior is concerned, lycaenid larvae mimics are normally specific to one species of host ant (Cottrell 1984; Thomas et al. 1989), which is probably due to a specificity in the chemical signals the ants use to recognize nest companions and brood (Hoelldobler & Carlin 1987). Although this species specificity of the lycaenid larvae towards their ant hosts may have led to a diversification of some genera (e.g., *Maculinea*, *Lepidochrysops*), this diversification is far lower than that of cooperative taxa, a finding that contradicts the hypotheses of Pierce (1984) who argued that species specificity should amplify the species diversity of the Lycaenids (see also discussion in Fiedler 1991b). Nonetheless, being associated with only one species of ant carries with it certain ecological disadvantages for the lycaenid larvae such as constraints on their distribution caused by a patchy distribution of their host ant species (Jordano et al. 1992), problems of host encounter in areas with a highly diverse ant fauna, and nutritional constraints (Fiedler 1991b). For the predaceous symphiles exploitative behavior also carries with it a high risk. Their host ants are generally tolerant of intruders in times of plenty, but when food reserves are low they become increasingly intolerant and will even eat their own brood (Thomas et al. 1989). The lycaenid larvae must therefore be under extreme pressure to mimic their hosts as closely as possible and it is not surprising that so few species have developed this type of relation.

4) We may speculate that parasites normally have much shorter life cycles

than their hosts, as for example viral or bacterial parasites on insect or mammal hosts. Thus, cooperative mechanisms are more likely to act in interactions between two species with equivalently long life cycles. The life-spans of ant workers and butterflies have roughly the same order of magnitude (they are measured in months). Even ant colonies do not live much longer, as in most species, the mean life span of queens and colonies is a few years. Thus exploitation of one by the other is evolutionarily unlikely.

In conclusion, a relatively high proportion of species seem to employ cooperative or mutualistic behavior in their associations with ants rather than exploitative or selfish behavior. We suggest that this pattern reflects the extraordinary stability of cooperative interactions in evolutionary terms, at least as regards lycaenid/ant interactions.

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